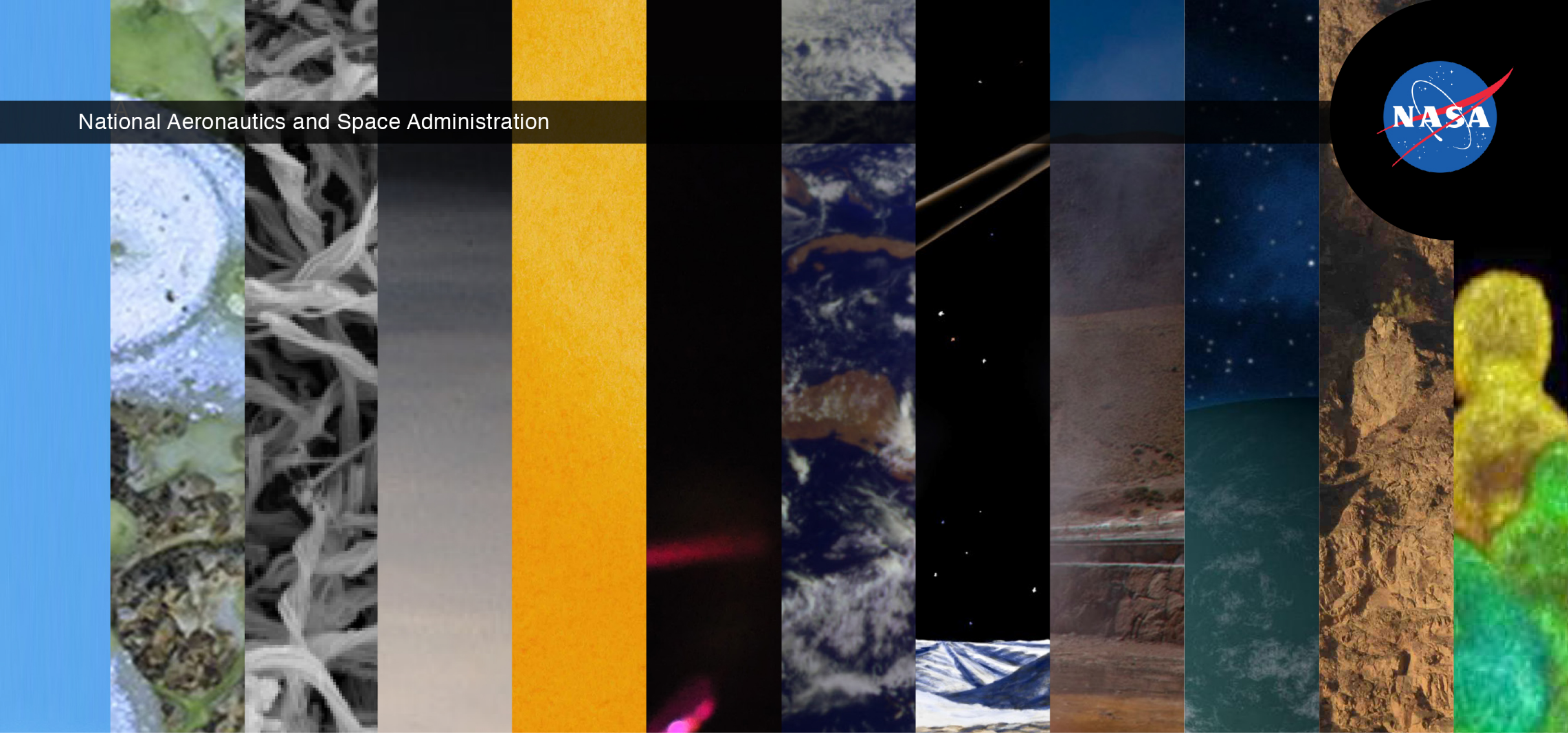
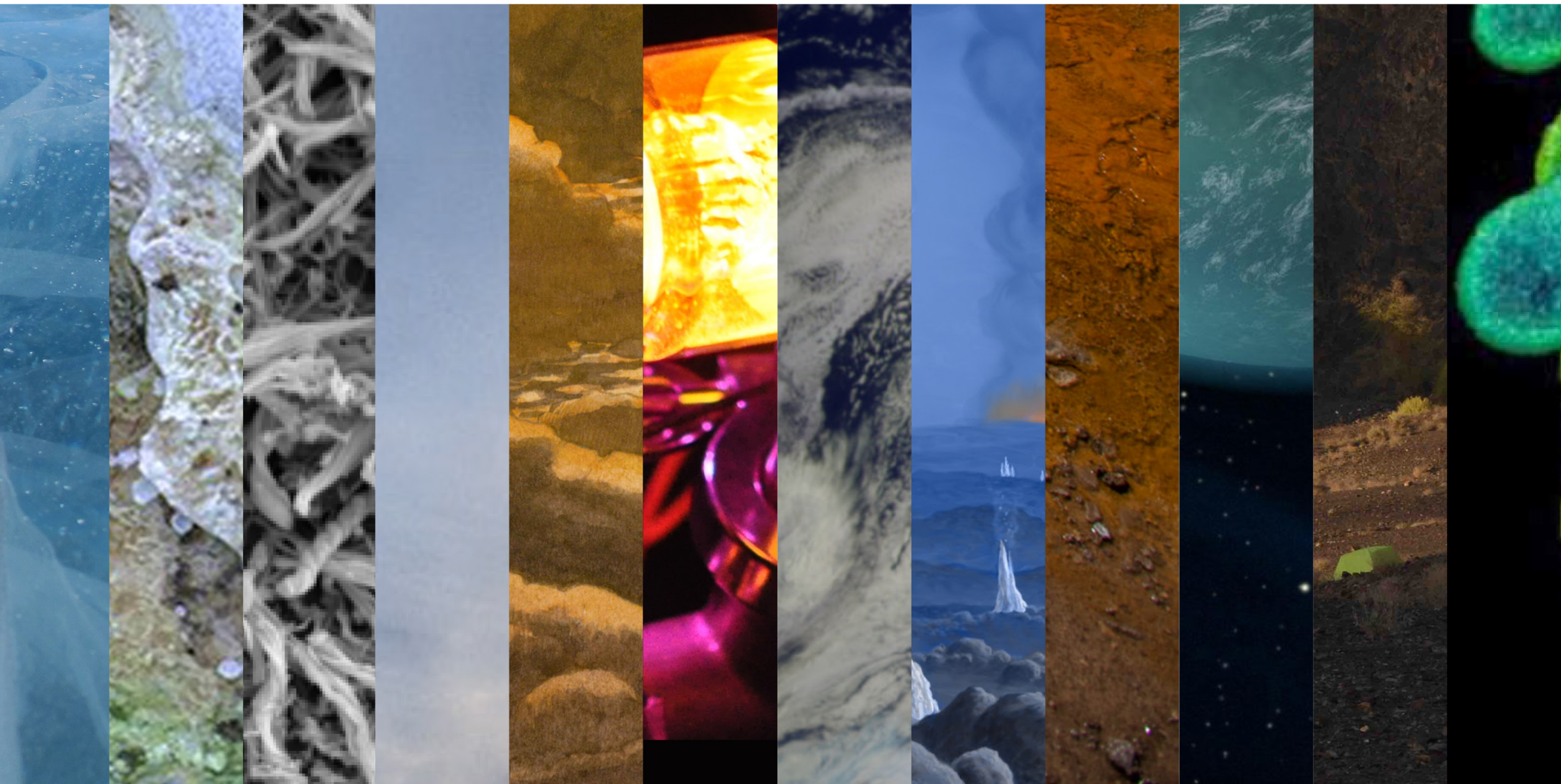


NASA Astrobiology Institute

2017 Annual Science Report

Foundations of Complex Life
Evolution, Preservation and Detection on Earth and Beyond

Massachusetts Institute of Technology



Foundations of Complex Life
Evolution, Preservation and Detection on Earth and Beyond

Lead Institution:
Massachusetts Institute of Technology

Principal Investigator:
Roger Summons

Team Overview

Foundations of Complex Life is a research project investigating the early evolution and preservation of complex life on Earth.

We seek insight into the early evolution and preservation of complex life by refining our ability to identify evidence of environmental and biological change in the late Mesoproterozoic to Neoproterozoic eras. Better understanding how signatures of life and environment are preserved will guide how and where to look for evidence for life elsewhere in the universe—directly supporting the Curiosity mission on Mars and helping set strategic goals for future explorations of solar system and studies of the early Earth.

Our Team pursues these questions under five themes:

I. *The earliest history of animals:* We use methods from molecular biology, experimental taphonomy, and paleontology to explore what caused the early divergence of animals.

II. *Paleontology, sedimentology, and geochemistry:* We track the origin of complex protists and animals from their biologically simple origins by documenting the stratigraphy, isotopic records, and microfossil assemblages of well-preserved rock successions from 1200 to 650 million years ago.

III. *A preservation-induced oxygen tipping point:* We investigate how changes in the preservation of organic carbon may have driven the Neoproterozoic oxygenation of the oceans coincident with the appearance of complex life.

IV. *Taphonomy and Curiosity:* As the Mars rover Curiosity explores Gale Crater we integrate research on Mars and Earth to understand Martian environments and geochemistry.

V. *Synthesis:* We seek to generate an expanded view of major transitions on Earth, environmental and biological, and apply this to develop a synthesis of the history of biological habitability on Mars.

Team Website: http://www.complex-life.org

2017 Executive Summary

Mars Geology and Geochemistry

MIT Team members have synthesized knowledge about biosignature preservation and submitted an extensive review of the conditions required to preserve traces of life on Mars. This should serve as a guide to likely targets for the 2020 Mars landing site selection.

MIT Team members Grotzinger, Sumner and Milliken, working with colleagues on the Mars Science Laboratory Mission, published their report integrating what has been learned about the ancient lacustrine environment in Gale Crater. Redox stratification of the lake water body, caused by depth-dependent variations in the concentration of atmospheric oxidants and dissolved, groundwater-derived solutes, resulted in oxidizing conditions in shallow water and anoxia in deeper water. This is further evidence of habitability of the Gale ancient lake environment.

Hannah Kaplan of the Milliken Lab at Brown University has been able to place better quantitative limits on how NIR reflectance spectroscopy can be used to detect organic matter in ancient shales on Earth and other planetary bodies from orbiting spacecraft. UC Davis student , Frances Rivera Hernandez, working with Dawn Sumner, developed, demonstrated, and applied a new statistical technique to use ChemCam data from the MSL mission to estimate sedimentary rock grain sizes. This technique will improve our interpretations of depositional environments for all the rocks Curiosity analyzes and can be used with SuperCam data for the Mars2020 mission.

Neoproterozoic Geology and Geochemistry

The Bergmann Lab at MIT has now reliably produced clumped isotope temperature data from Neoproterozoic to Ordovician carbonates. They are using these direct measures of temperature to inform our understanding of Neoproterozoic events and are coupling them to other geochemical data and carbon cycle modeling efforts. In complementary studies, Johnston, Macdonald and their teams have begun making minor oxygen isotope measurements of Marinoan age barite deposits from Northwest Canada to test the stratigraphic and basinal variability in the preserved ^{17}O anomaly. The magnitude of this anomaly has been argued to scale with atmospheric pCO_2.

Proterozoic Paleontology

Graduate students Sharon Newman and Kelsey Moore published *Geobiology* articles that describe the preservation of cyanobacterial and eukaryotic fossils by the interactions between organic matter and clay minerals. Newman also used experimental taphonomy to demonstrate that the formation of clay mineral veneers delays the decay of soft tissues surrounded by kaolinite. Moore reported pyritized microbial fossils in the Cryogenian carbonates from Arctic Alaska.

Research in the Cohen Lab has documented the oldest presently known evidence of primary eukaryotic biomineralization in the fossil record and has tied this evolutionary innovation to changing oceanographic conditions of the Neoproterozoic. They have also described and documented a new species of fossilized testate amoeba from strata directly preceding the first "Snowball Earth" event and revealed new information on how such fossils are preserved and their role in our understanding of eukaryotic diversification. Finally, they are documenting new algal fossils from in between the two "Snowball Earth" events and have identified two distinct life cycles in a fossil red alga.

Team members also reported a new three-dimensionally preserved phosphatized Doushantuo-type microfossil assemblage, with probably multicellular embryos, from the latest Ediacaran of Mongolia illustrating the potential of the Khuvsgul Group to provide new data on early animal evolution. They also reported the most completely preserved examples of a fossil chaetognath (Phylum Chaetognatha) with details of the soft parts - from the 508-million-year old Burgess Shale – which is distinct from all other forms by having about 25 spines in each half of its predatory apparatus.

Knoll and Javaux provide a state-of-the art description of eukaryotic microfossils in mid-Proterozoic oceans. Because of earlier stratigraphic research, they were able to evaluate

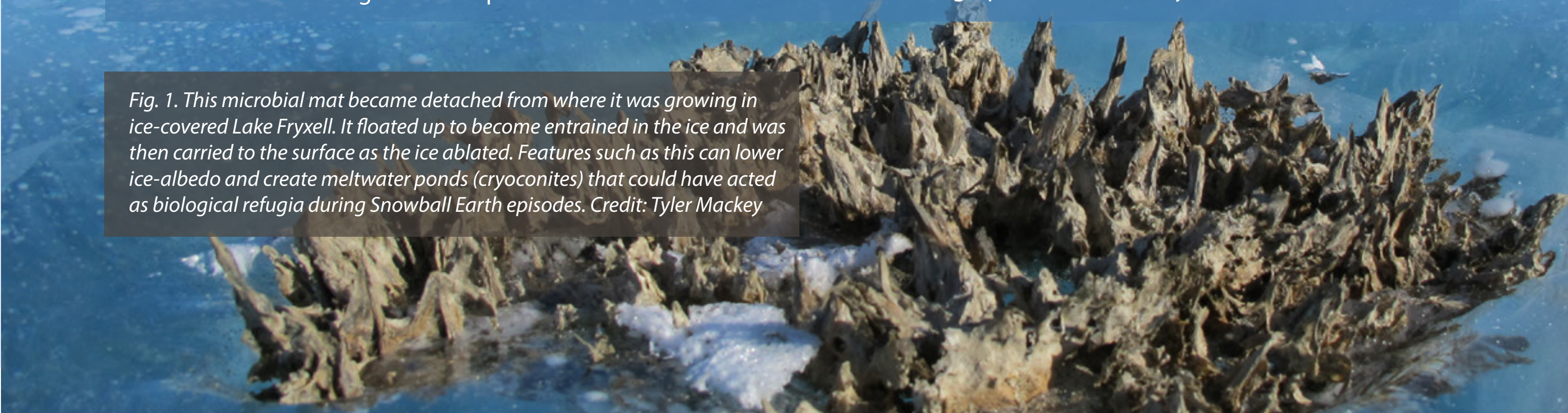


Fig. 1. This microbial mat became detached from where it was growing in ice-covered Lake Fryxell. It floated up to become entrained in the ice and was then carried to the surface as the ice ablated. Features such as this can lower ice-albedo and create meltwater ponds (cryoconites) that could have acted as biological refugia during Snowball Earth episodes. Credit: Tyler Mackey

these fossils in the context of both their environmental distribution in a 1500-1400 Ma seaway and in terms of mid-Proterozoic global trends in marine ecosystems.

Erwin made substantial progress on a book on evolutionary novelty and innovation. Several of the papers just published represent components of this work. McInerney and Erwin present an argument for the involvement of public goods in novelty and innovation. Also notable was work of Emmy Smith (now an Asst. Professor at Johns Hopkins) on new Ediacaran faunas in Nevada and possible Ediacaran-Cambrian boundary localities.

Phylogenomics of Complex Life

Members of the Fournier Lab have finalized the results of three independent molecular clock investigations using multiple models for dating the early evolutionary history of Cyanobacteria. These projects utilized up-to-date phylogenies, newly sequenced cyanobacterial lineages, and new cyanobacterial microfossil data, as well as two novel techniques for adding horizontal gene transfer events as informative constraints on the timing of microbial evolution. These results consistently support an early diversification of cyanobacteria around or shortly before the Great Oxygenation Event ~2.33 Ga (2.6-2.2 Ga), with stem cyanobacteria diverging from non-photosynthetic ancestors ~3 Ga, an improvement in precision over previous estimates, and independent of any geochemical assumptions being used as date calibrations.

Peterson and colleagues are nearly ready to release MirGeneDB 2.0 (http://mirgenedb.org:82/), which now contains 28 species and 7359 hand-currated bona fide microRNAs detailing orthology and paralogy relationships (as well as the evolutionary origins) of all microRNA genes and families, expression atlases for tissues (where available), motif distributions, genomic coordinates, processing variants, and links to all major microRNA databases and genome atlases. This tool will be invaluable to researchers wanting to work on the expression, processing, and evolution of bona fide microRNAs without having to worry about mis-annotations including RNA fragments derived from non-miRNA genes.

The Carbon Cycle and Complex Life

Rothman completed an empirical study of carbon isotopic excursions through geologic time. The results identify a critical rate of change beyond which mass extinction occurs. Work in progress has identified a mechanism through which the carbon cycle may undergo one or more major excitations while its steady state remains stable.

Biosignature Research

Members of the Pearson Lab showed that carbon isotope fractionation in a dinoflagellate is identical to that of diatoms and haptophytes. This is unexpected, because diatoms and haptophytes have Form 1D Rubisco, while the dinoflagellate has Form II. Using this information, they are now working on a new model that would fundamentally change the view of how carbon is fixed by eukaryotic algae. This model suggests that carbon isotope effects are controlled by the balance between the photosynthetic rate and the growth rate, which fundamentally control intra- and extra-cellular carbon exchange rates. This implies that the canonical 25 permil fractionation of marine organic matter is unrelated to the enzyme Rubisco.

In collaboration with members of the Australian Centre for Astrobiology and researchers from PSU and University of Colorado, Summons Lab members investigated the structures of bacteriohopane polyols in relation to environmental conditions. We identified that the occurrence of an unusual bacteriohopane polyol is a biomarker for water column and sediment redox and determined potential physiological roles for cyanobacterial 2-methylbacteriohopane polyols.

Fieldwork

Since January, members of the Macdonald and Briggs groups embarked on new fieldwork in northern Mongolia to provide more geological context to the newly discovered animal embryo fossils described in Anderson et al. (2017). Macdonald's team also began new fieldwork in Namibia where they are developing new geochronological constraints on the duration of the Marinoan glaciation and the tempo of the Ediacaran-Cambrian transition.

Bergmann, Mackey and others conducted field expeditions worldwide to continue to build a suite of shallowly buried Neoproterozoic-Ordovician samples from Svalbard, Newfoundland, Anticosti Island, and the Upper Midwest.

Analogue Studies

Members of the Sumner Lab continued their work on microbial communities of lakes in the McMurdo Dry Valleys, Antarctica which serve as analogs for Cryogenian biological oases.

Fig. 2. Members of a field expedition collect shallowly buried and well preserved Neoproterozoic sedimentary rock samples from Svalbard. Credit: Tyler Mackey

Project Reports

Neoproterozoic Paleontology

The Bosak Lab described how the interactions between organic matter and clay minerals preserve cyanobacterial mats on the surfaces of sandstones and siltstones (Newman et al., *Geobiology*, 2017). They also provided evidence for the global distribution of agglutinating microscopic eukaryotes between the Sturtian and the Marinoan glaciation (Moore et al., *Geobiology*, 2017) and pyritized cyanobacterial fossils in the Cryogenian carbonates from Arctic Alaska (Moore et al., Palaios, in press). Three members of the lab contributed insights into microbial fossilization in the collaborative review article about where to look for fossils on Mars (McMahon et al., *Journal of Geophysical Research,* 2018).

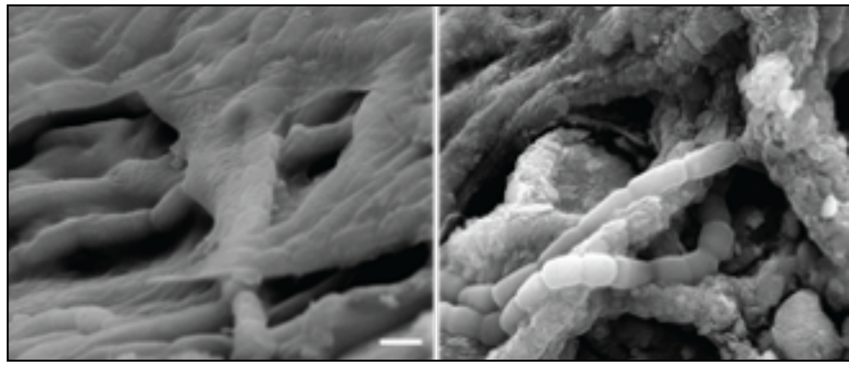


Fig. 3. Electron micrographs of mat-forming cyanobacteria coated by clay minerals (from Newman et al., 2017). Left: Smoothly coated cyanobacteria incubated on sand, Right: Coated and uncoated filamentous cyanobacteria incubated on illite. Scale bars: 1 µm.

The Cohen Lab has documented the first evidence of primary eukaryotic biomineralization in the fossil record (Cohen et al., *Science Advances*, 2017) and a new species of fossilized testate amoeba from strata directly preceding the first "Snowball Earth" event (Cohen et al., *Palaeontology*, 2017).

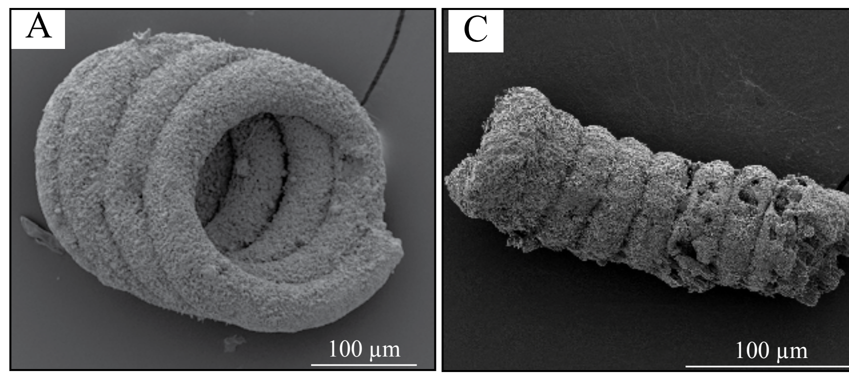


Fig. 4. Electron micrograph of pyritized cyanobacterial fossil <u>*Obruchevella*</u> *from Arctic Alaska (from Moore et al., 2017).*

Team members also reported a new three-dimensionally preserved phosphatized Doushantuo-type microfossil assemblage, with probable multicellular embryos, providing new data on early animal evolution in the later Ediacaran (Anderson et al., *J. Syst. Paleontol*., in review). They also reported the most completely preserved examples of a fossil chaetognath (Phylum Chaetognatha) with details of the soft parts - from the 508-million-year old Burgess Shale – which is distinct from all other forms by having about 25 spines in each half of its predatory apparatus (Briggs et al., *Curr. Biol*., 2017).

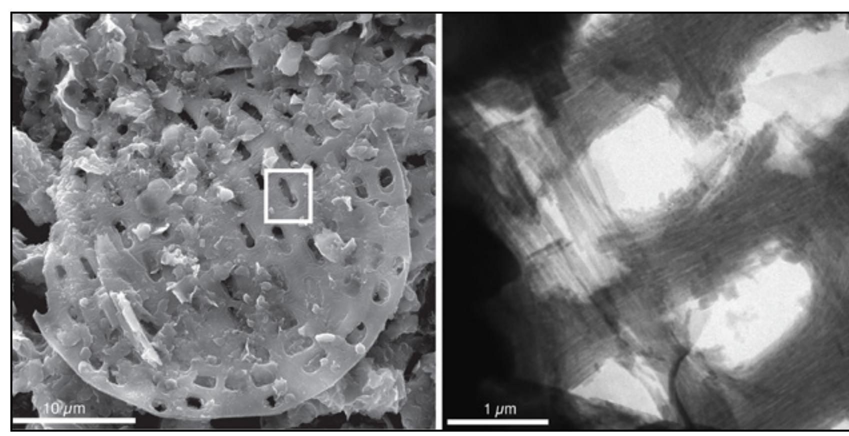


Fig. 5. Electron micrographs of biomineralized fossils from the Yukon. Left: scanning electron micrograph of single mineralized fossil. Right: high resolution transmission electron micrograph of the area in white box at left showing interwoven fibers of hydroxyapatite minerals (from Cohen et al., 2017).

Knoll and Javaux evaluated 1500-1400 Ma eukaryotic fossils in the context of environmental distribution and in terms of mid-Proterozoic global trends in marine ecosystems (Javaux and Knoll, *Journal of Palaeontol*., 2017).

Erwin is writing a book on evolutionary novelty and innovation that includes several of the just published papers. Emmy Smith (now an Asst. Professor at Johns Hopkins) reported on new Ediacaran faunas in Nevada and possible Ediacaran-Cambrian boundary localities.

Mission to Mars

NASA's *Curiosity* rover was designed to assess a local region on Mars' surface as a potential habitat for past life. The Gale crater landing site hosts thick and diverse sedimentary rocks that preserve evidence for a lake environment that was sustained for tens of thousands to tens of millions of years. The Murray formation comprises the principal lacustrine unit studied to date and represents two distinct settings. On the basis of mineralogy, geochemistry, and textural properties, the Murray formation can be subdivided into two facies: the Hematite-Phyllosilicate (HP) facies, and the Magnetite-Silica (MS) facies. The HP facies is characterized by abundant Fe^{3+}-oxides accompanied by phyllosilicates, as well as indications of Mn-oxidation and trace metal concentration. These properties are consistent with deposition in an oxidizing environment. The MS facies is recognized by a near-complete absence of Fe^{3+}-minerals, and high concentrations of silica accompanied by magnetite, consistent with deposition in an anoxic environment. The distinct properties of the two Murray facies were developed as a result of: (i) deceleration of river-flow entering the lake, which resulted in the fractionation of river-borne detritus into coarser, denser materials in shallow water close to shore, and finer, lower density materials offshore in deeper water; (ii) redox stratification of the lake water body, caused by depth-dependent variations in the concentration of atmospheric oxidants and dissolved, groundwater-derived solutes, resulting in oxidizing conditions in shallow water, and anoxia in deeper water. The recognition of redox stratification in the Gale crater lake adds new detail to our understanding of ancient Martian aquatic environments and providing compelling evidence that all of the physical, chemical, and energetic conditions necessary to establish a habitable environment were present on Mars at ca. 3.5 Ga.

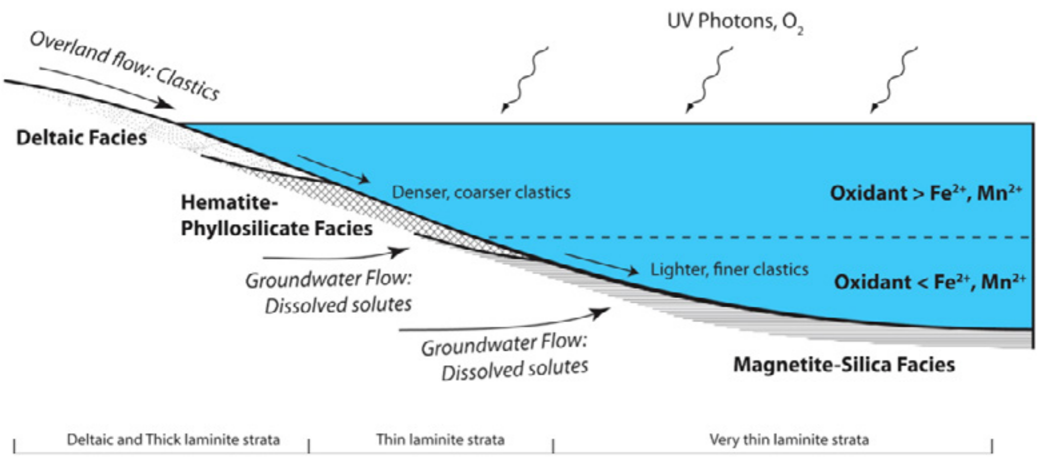


Fig. 6. Model of physical transport and geochemical processes active during deposition of the Murray formation. Fresh water and clastic materials are delivered by overland flow from fluvial systems, dissolved solutes enter the lake by groundwater seepage. Flow deceleration results in sediment fractionation; coarser, denser clastic materials are deposited closer to shore, while finer, less dense clastics travel further into the lake. Stratification results from differences in the mass balance of atmospheric oxidants (ultraviolet photons, O_2) and oxidizable cations (Fe^{2+}, Mn^{2+}), causing redox sensitive mineral assemblages to vary as a function of lake water depth.

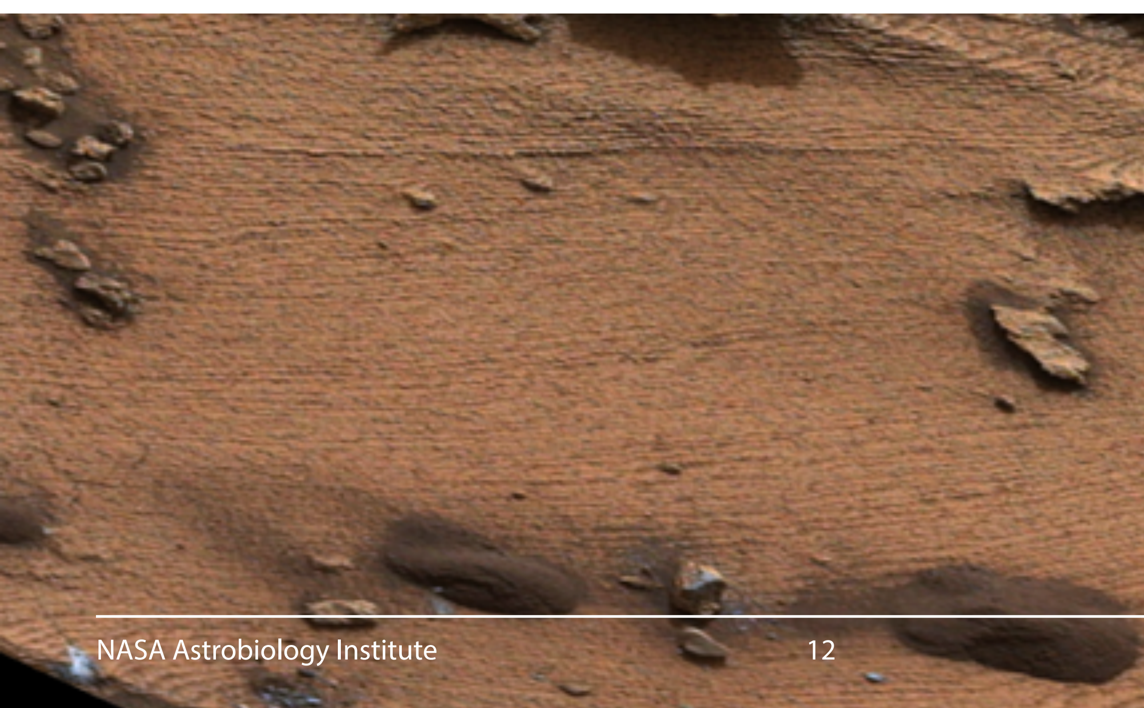


Fig. 7. Finely-laminated Murray formation mudstone formed by settling of fine-grained sediments derived from plumes entering the Gale lake. In addition, chemical sediments enriched in Fe3+-oxides and clay minerals also precipitated from stratified waters, creating an oxidizing environment.

Thresholds of Catastrophe in the Earth System

Daniel Rothman has analyzed significant changes in the carbon cycle over the last 540 million years, including the five mass extinction events. He has identified "thresholds of catastrophe" in the carbon cycle that, if exceeded, would lead to an unstable environment, and ultimately, mass extinction.

In his recent paper, "Thresholds of catastrophe in the Earth system," published in Science Advances, Rothman proposes that mass extinction occurs if one of two thresholds are crossed: For changes in the carbon cycle that occur over long timescales, extinctions will follow if those changes occur at rates faster than global ecosystems can adapt. For carbon perturbations that take place over shorter timescales, the pace of carbon-cycle changes will not matter; instead, the size or magnitude of the change will determine the likelihood of an extinction event.

Taking this reasoning forward in time, Rothman predicts that, given the recent rise in carbon dioxide emissions over a relatively short timescale, a sixth extinction will depend on whether a critical amount of carbon is added to the oceans. That amount, he calculates, is about 310 gigatons, which he estimates to be roughly equivalent to the amount of carbon that human activities will have added to the world's oceans by the year 2100.

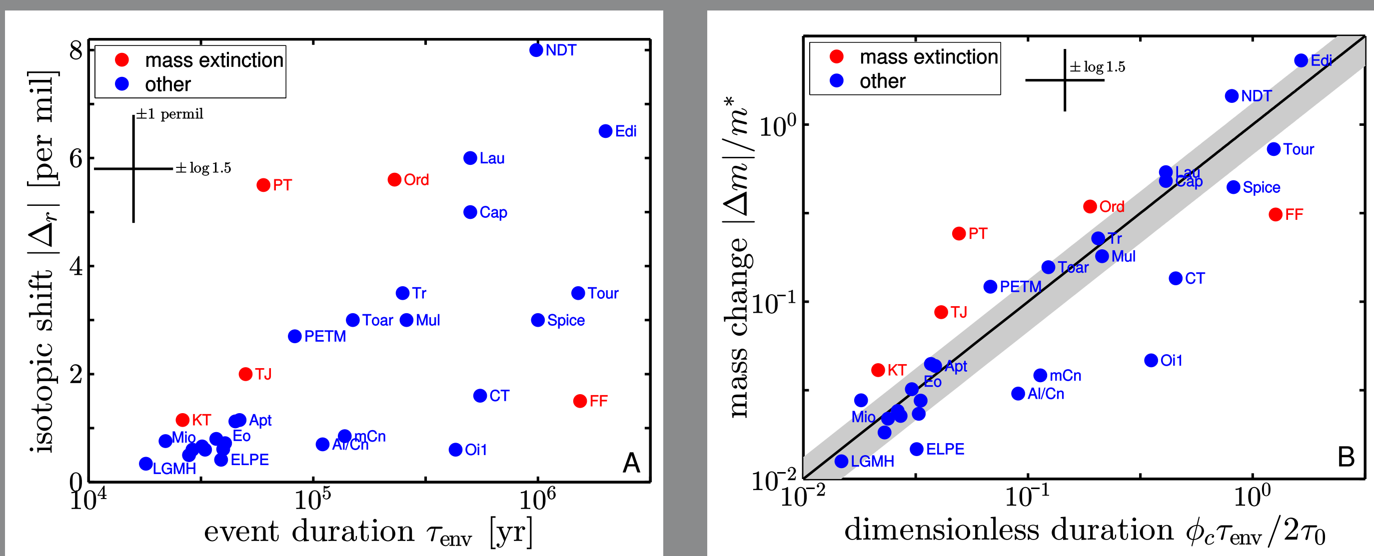


Fig. 8. The size and timescale of 31 carbon-isotopic events during the last 540 million years. (A) The magnitude of carbon isotopic shifts as a function of their duration of time. (B) The dimensionless mass perturbation as a function of the dimensionless timescale for each of the events depicted in (A). The straight (identity) line denotes a theoretical prediction.

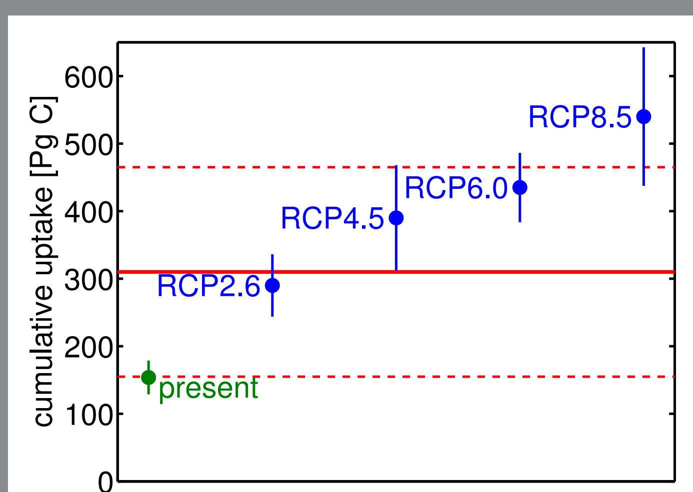


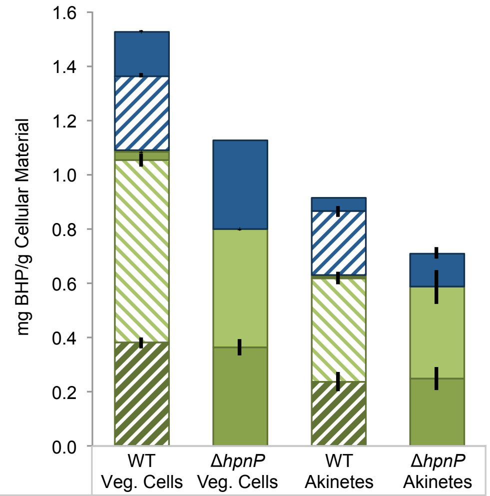
Fig. 9. Cumulative modern ocean uptake of carbon since 1850, up to the present (green) and projected to 2100 (blue), compared to the predicted critical mass of 310 Pg C (solid red line) and an assumed 50% uncertainty (dashed red lines). Projections are given for four representative concentration pathway scenarios spanning the full range of emissions scenarios in the scientific literature.

Biosignature Research

2-Methylhopane hydrocarbons are an enigmatic feature of the chemical fossil record because they occur in high concentrations in black shales deposited through oceanic anoxic events and across major extinction horizons. Yet their origin and meaning is vigorously debated. To address these questions we investigated the function of 2-methylhopanoids in some modern cyanobacteria and cyanobacterially-dominated ecosystems.

In one study (Garby et al., 2017), the hpnP gene coding for the radical SAM methylase protein that acts on the C2 position of hopanoids, was deleted from the filamentous cyanobacterium Nostoc punctiforme ATCC 29133S. The resulting ΔhpnP mutant lacked all 2-methylhopanoids, but was found to compensate by producing much higher levels of two bacteriohopanepentol isomers compared to the wild type (Fig. 11). The relative abundances of the different hopanoid structures in akinete-dominated cultures of the wild-type and ΔhpnP mutant were similar to those of vegetative cell-dominated cultures (Fig. 11) . Growth rates of ΔhpnP mutant cultures were not significantly different from those of the wild type under standard growth conditions and akinete formation was also not impeded by the absence of 2-methylhopanoids (Fig. 12). However, the ΔhpnP mutant was found to have decreased growth rates under both pH and osmotic stress, confirming a role for 2-methylhopanoids in stress tolerance. Evidence of elevated photosystem II yield and NAD(P)H-dependent oxidoreductase activity in the ΔhpnP mutant under stress conditions, compared to the wild type, suggested that the absence of 2-methylhopanoids increases cellular metabolic rates under stress conditions.

In collaboration with members of the former CAN4 team if the NAI based at Penn State University we also completed a study (Hamilton et al., 2017) of the abundances of 2-methylhopanoids in an unusual natural environmental sample. A red pinnacle mat in Little Salt Spring (Sarasota County, FL, USA) occurs where light is limited and the entire water column experiences sulfidic (~50 µM) conditions seasonally, resulting in a system poised between oxic and sulfidic conditions. Abundant 2-methylhopanoids of cyanobacterial origin formed under conditions of low oxygen and low light are consistent with the recovery of these structures from ancient black shales as well as their paucity in modern marine environments.



	WT Veg. Cells	ΔhpnP Veg. Cells	WT Akinetes	ΔhpnP Akinetes
BHT	0.163	0.330	0.052	0.124
2-MeBHT	0.272	0.000	0.236	0.000
BHpentol-1	0.011	0.434	0.003	0.338
BHpentol-2	0.027	0.363	0.006	0.249
2-MeBHpentol-1	0.675	0.000	0.382	0.000
2-MeBHpentol-2	0.379	0.000	0.237	0.000

Fig. 11. Abundance of hopanoids in cultures of wild type and mutant Nostoc punctiforme as analyzed by LC-MS. The lipid content of wild-type (WT) and ΔhpnP cultures dominated by late exponential phase vegetative cells or akineteswas characterized. Hopanoids (mg BHPs/g cellular material) detected in each sample is given below the cellular type. Quantification was completed using authentic deuterium-labeled BHtetrol and 2-MeBHtetrol standards. Values were averaged from 2 LC-MS runs (June 4, 2014 and June 16, 2015). Error bars represent 1 standard deviation.

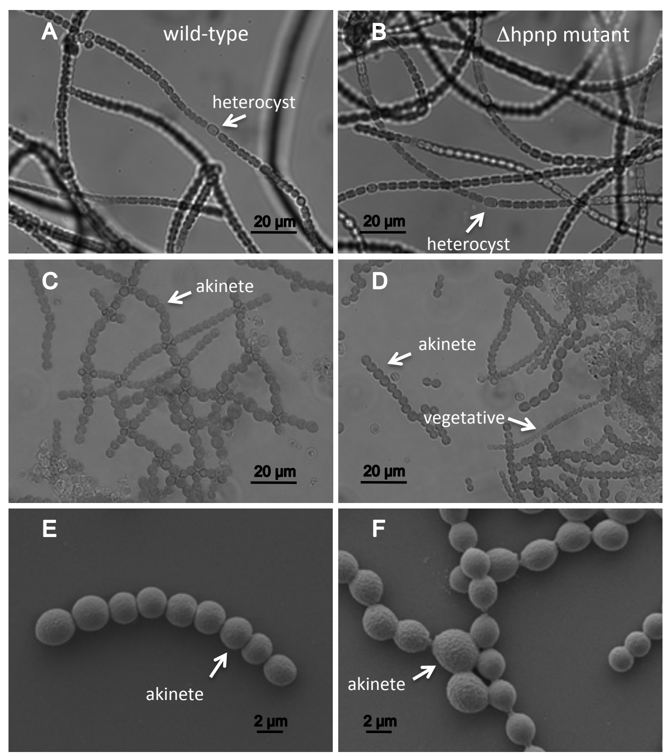


Fig. 12. Differential interference contrast micrographs (A-D) and SEM images (E, F) of cultures of wild-type N. punctiforme (A, C, E) and the ΔhpnP mutant (B, D, F), under control conditions (A, B) showing vegetative cell filaments with heterocysts, and sixteen weeks after transfer t o phosphate-free medium and low light conditions (C-F), showing formation of akinetes amongst vegetative filaments.

Team Members

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Field Work

Geological Records of Complex Life

Our Team explores the geological record of life between ~ 1.5 and 0.54 billion years ago. We reconstruct environmental records of this critical interval and work to understand the geological context of the development of complex life.

Over the reporting period our Team has conducted field campaigns in Mongolia, NW Territories of Canada, China, Namibia, Newfoundland, Svalbard and the Southwestern US. Many of these sites have time equivalent strata. Work in these diverse yet comparable locations aims to build a more global picture of different environments and the life contained in them across the various diversification events of complex life.

We also conducted research on samples collected from the McMurdo Dry Valleys of Antarctica. Samples from ice-covered lakes and cryoconites serve as analogues for biological refugia that must have existed during the Cryogeian epoch.

Image Credit: Roger Summons

Foundations of Complex Life: 2017 Publications

Anderson, R. P., Macdonald, F. A., Jones, D. S., McMahon, S. and Briggs, D. E. G. (2017). Doushantuo-type microfossils from latest Ediacaran phosphorites of northern Mongolia. *Geology,* 45: 1079-1082. DOI:10.1130/G39576.1.

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